EGG COMPARISONS AND VOLUME ESTIMATION METHODS BETWEEN THE COMMON MUSK TURTLE (KINOSTERNIDAE: *STERNOTHERUS ODORATUS*) AND THE TEXAS TORTOISE (TESTUDINIDAE: *GOPHERUS BERLANDIERI*)

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Egg volume, extensively studied in birds, has been largely overlooked in reptiles. This measurement is a valuable estimator of fresh egg weight, which could predict multiple physiological parameters. Morphological constraints of adult female turtles on egg size, shape and number result in production of a broad range of shapes and sizes. Eggs of *Sternotherus odoratus* and *Gopherus berlandieri* were used to determine the most accurate method of volume estimation alongside shape and size comparisons among species. Dimensional measurements of *Kinosternon flavescens* eggs were used for comparative purposes to *Sternotherus.* The most accurate method of volume estimation in *Sternotherus* was the ellipsoid formula (Iverson and Ewert, 1991), but the bicone method best approximated *Gopherus* egg volume (Preston, 1974). The elongation factor, a measure of increased cylindrical length, was 1.7 in *Sternotherus* compared to an index of 1.2 in *Gopherus,* thus quantifying the nearly round aspect of *Gopherus* eggs. When compared to *Kinosternon*, eggs of *Sternotherus* differed only in diameter; eggs of these species did not statistically differ in length or volume. *Kinosternon* produces eggs comparable in individual size and volume to eggs of *Sternotherus*, but is capable of producing more eggs per clutch resulting in a greater clutch volume.

INTRODUCTION

Approximately 250 turtle species currently are recognized by Pough et al. (1999). Despite considerable systematic work that has been done, little is known about the life history characteristics of a vast number of these species (Ernst et al., 1994). Careful investigation of egg parameters is necessary to effectively elucidate reproductive biology, because most reproductive effort in turtles is expended in forming, expelling, and burying the eggs. Optimal egg size theories predict that turtles should produce many small eggs or relatively few larger ones, a pattern observed in aquatic versus terrestrial species (Smith and Fretwell, 1974). A larger individual reproductive product, or egg, might portend greater offspring fitness (Brockelman, 1975; Congdon and Gibbons, 1985). However, egg size, and therefore offspring size, is constrained in many turtles because eggs must pass through the pelvis and exit the shell. Leathery eggshells and carapace-plastron kinesis lessen somewhat egg size constraints imposed by the bony shell. Aquatic turtles lay either hard-shelled or leathery-shelled eggs, but terrestrially adapted turtles such as tortoises and box turtles, lay hard-shelled eggs. In this study, I compared the egg volume parameters of two species of turtle, one aquatic and the other terrestrial. Both produce porcelain-hard eggshells, but they are of radically different shape. I also included dimensional data of eggs collected from a population of *Kinosternon flavescens* (Rose, unpublished data) for intrafamilial comparison with *S. odoratus*.

The common musk turtle or stinkpot, *Sternotherus odoratus* (Testudines: Kinosternidae), is a small freshwater species distributed across the eastern half of North America. In southern populations of stinkpots, the average number of eggs per clutch is 2.2 and females are capable of producing multiple clutches per year (Tinkle, 1961). Stinkpot eggs are elliptical in shape with blunted ends and are brittle shelled (Ernst et al., 1994). Selective pressures, before and after laying, that favor a larger sized reproductive product most likely produce this ellipsoid shape (Rose et al., 1996). Average oviducal egg size in a Virginia population was 26.7 mm in length and 15.9 mm in width, indicating a large degree of elongation (McPherson and Marion, 1981).

The Texas tortoise, *Gopherus berlandieri* (Testudines: Testudinidae) is a small to medium-sized terrestrial turtle found in South Texas and Northern Mexico. Females are capable of laying both spherical and ellipsoid eggs, and there is an inverse relationship between mean clutch size and degree of elongation (Judd and Rose, 1989). Clutch sizes range from 1 to 5 with no correlation between clutch and female size (Judd and Rose, 1989).

The yellow mud turtle, *Kinosternon flavescens*, is a bottom-dwelling turtle ranging through the eastern two-thirds of Texas, north to Nebraska, west to New Mexico and Arizona, and south into Mexico (Ernst et al.,1994). Each clutch consists of 1 to 9 hard elliptical eggs (Iverson, 1991). Pelvic aperture in this species are larger in females and allow for passage of larger eggs (Long and Rose, 1989).

Reproductive effort is the proportion of an organism's energy budget devoted to reproductive processes (Hirshfield and Tinkle, 1975). In most species of oviparous reptiles, each egg can be considered representative of the majority of parental investment per offspring (Congdon and Gibbons, 1983). Egg material supplies energy for development and subsequently serves as storage for hatchling maintenance (Congdon and Gibbons, 1983; Congdon et al., 1983). According to Brockelman (1975) females can increase the survivorship and competitive ability by allocating greater energy per offspring. Consequently, egg size has been optimized via natural selection to the point that increased fitness from greater investment per offspring is equal to the decline in fitness associated with the reduced number of offspring (Smith and Fretwell, 1974). If proposed models of optimal egg size are correct, most change in reproductive output within a population should result in greater offspring number rather than an increase in size (Congdon and Gibbons, 1985). Furthermore, optimal egg sizes should be most evident in species with large clutch sizes and no post-ovulatory parental care (Congdon and Gibbons, 1985). Additional material added to each egg, however, might have a negative effect on clutch size as any fitness loss due to reduction in offspring number is offset by the increased survival of larger offspring (Congdon and Gibbons, 1985).

A positive correlation exists between reproductive output and body size in turtles, where constraints placed on egg size limit offspring size (Gibbons et al., 1982; Congdon and Gibbons, 1987; Moll, 1979). Observed variability and inconsistency observed between clutch size and body size are primarily a function of maternal body size, which sets an upper limit on the number of eggs of a given size per clutch (Gibbons et al., 1982). There is a negative relationship between egg size and clutch size within a species, which, in itself, is not direct evidence for egg size tradeoff predicted by optimal egg size models (Congdon and Gibbons, 1987). Some species of freshwater turtle, such as *Chrysemys picta* (western painted turtle) and *Deirochelys reticularia* (chicken turtle), are unable to produce eggs of the size and number that are predicted by optimal egg size theories (Congdon and Gibbons, 1987).

Morphological constraints of female turtles prohibit enlargement of eggs in diameter, which prevents eggs from reaching maximal and optimal width (Congdon and Tinkle, 1982). Egg size in turtles is constrained by the size of the pelvic girdle and the carapace-plastron exit port (Congdon and Gibbons, 1987; Rose and Judd, 1991). The pelvic girdle of turtles is subject to selective pressures for locomotion and limb retraction that work against those of reproduction (Congdon and Gibbons, 1987). Variation in egg size of turtles can be reconciled with optimal egg size theory only if a pelvic constraints model is accepted (Congdon and Gibbons, 1985). Congdon and Gibbons (1987) found a correspondence in regression slopes of the increase of pelvic aperture and egg width with increasing body size, and concluded that most variation in turtle egg size appeared to be associated with female body size. Each millimeter of increase in pelvic opening is accompanied by an equivalent increase in egg width leading to the assumption that hatchlings of smaller females are negatively affected (Congdon and Gibbons, 1987; Congdon et al., 1983). In some species, such as *Gopherus berlandieri*, pelvic aperture is quite large, but in its normal state, diameter of the carapace-plastron exit port is insufficient to pass eggs (Rose and Judd, 1991), who found that eggs of this species forced the xiphipastra ventrally and the posterior carapace dorsally enlarging the exit port.

Egg shape modification might be a means by which species overcome morphological constraints (Hailey and Loumbardis, 1988). Eggs can be spherical, elongate to differing degrees or pillow-shaped (Agassiz, 1857). Spherical eggs may be an adaptation for packing large numbers of eggs into the oviducts of the female (Ewert, 1979). Volume can be increased most efficiently by increasing the diameter of a sphere, i.e. egg width, than is possible by elongation (Rose et al., 1996). Elongation also produces an increase in required calcium due to increased surface area, requiring an even greater energy input by the female (Rose et al., 1996). Egg width was found to be dependent on body size in individuals of the genus *Testudo* (tortoises) with smaller individuals producing narrower eggs that are more elongate, but having similar weight to those of larger individuals (Hailey and Loumbardis, 1988). Species producing large eggs relative to body size should demonstrate elongation of eggs to compensate for morphological constraints prohibiting enlargement of eggs in diameter and preventing eggs from reaching optimal egg width (Hailey and Loumbardis, 1988; Congdon and Tinkle, 1982). Elongated eggs of this type could provide a greater volume for each egg (Rose et al., 1996). The majority of egg mass increase due to elongation would be additional albumin and water. This implies that increased egg length is at least a limited option for increasing egg size and volume (Congdon et al,. 1983).

Mitchell (1985) noted that egg width was positively correlated to parental body size and was less variable than egg length in *Sternotherus odoratus* and *Chrysemys picta*. There also was less variation in egg width than in egg length among individuals. Clutch size was negatively correlated to egg length while positively correlated to egg width (Mitchell, 1985). The Virginia population studied by Mitchell (1985) demonstrated egg width constraint with variation in length. Thus, this species may provide useful in gathering additional data in the form of egg dimensions and volume measurements and relating these to reproductive output.

Egg volume has been extensively studied in birds, but research on reptiles, especially turtles is scant (Moll, 1979). Fresh egg weight is a useful predictor of parameters such as incubation period, water vapor conductance, daily rate of water loss, surface area, density, shell weight and the relationship between egg weight and adult body weight in birds (Hoyt, 1979). Unfortunately, fresh egg weight is difficult to determine because upon laying, the egg immediately begins to lose water and therefore, weight. Egg shape and size, however, are not altered by loss in egg volume and can be used to estimate fresh weight (Hoyt, 1979). In species such as *S. odoratus* and *G. berlandieri*, dehydration of the mineral layer does not alter the shape of the egg because the shells are brittle (Ewert, 1979). Volume is a function of egg shape, and determination may be a valuable predictor of egg physiology (Hoyt, 1979). According to Ewert (1979), hatchling size can be estimated as it corresponds to egg size when the form of measurement is weight.

Egg volume can be determined by three formulae: cylinder, ellipsoid and bicone (Rose et al., 1996; Iverson and Ewert, 1991). The cylinder formula assumes that an egg is cylinder shaped and both ends are hemispheres combined with diameter equal to egg width (Rose et al., 1996; Iverson and Ewert, 1991). This method overestimates volume (Rose et al., 1996; Iverson and Ewert, 1991). The ellipsoid method assumes that the egg is shaped as an ellipse and does not account for bluntness on either end. While more accurate than the cylinder method, it tends to underestimate volume (Rose et al., 1996; Iverson and Ewert, 1991). In practical tests, however, this method was found to be the best estimator of egg volume of *Pseudemys texana* (Texas river cooter) (Rose et al., 1996). The bicone method has proven to be the most accurate when using species specific bicone values, although this method does tend to underestimate volume (Iverson and Ewert, 1991). Bicone values are positively related to egg elongation and length and are negative for eggs with pointed ends, zero for ellipses, and positive for those with blunted ends (Preston, 1974).

Water displacement in a graduated cylinder is a method often used to estimate volume (Rose et al., 1996; McPherson and Marion, 1981). This is a common method used by avian biologists who have developed a field apparatus for measuring displacement (Thomas and Lumsden, 1981; Morris and Chardin, 1986). Another estimation technique used is internal volume determination

(Rose et al., 1996). The egg is emptied of material and the shell filled to determine the amount of water held. This value is considered the most valuable estimation, but is not feasible for broad utilization because it potentially causes death to embryos.

The purpose of this study is to determine the most accurate non-lethal method of estimating egg volume for *S. odoratus* and *G. berlandieri*. In order to make this determination, it was necessary to sacrifice embryonic turtles of both species. Inter- and intraclutch dimensions as well as egg shape differences were studied in both species and compared across clutches. I address egg dimension differences between *S. odoratus* and the closely related species *Kinosternon flavescens*, (yellow mud turtle) as well as the surface area of elongate eggs versus spherical eggs of the same volume.

MATERIALS AND METHODS

Eggs were collected from nests of *S. odoratus* at Aquarena Center, San Marcos, Hays County, Texas, on May 21, 2000 (IACUC 99-17, 99-14). Eggs were removed from nests and labeled according to clutch and egg number. Within two hours of collection, the eggs were cleaned, dried and measured with Mitutoyo digimatic calipers to the nearest 0.01 mm in both diameter and length. Mass of each egg was determined to the nearest 0.1 g using an electronic Mettler BasBal scale. Displacement of water was determined to the nearest 0.05 ml using a 100 ml graduated cylinder.

Egg volume was measured by using a probe to open a hole approximately 1 mm in diameter at one end of the egg. A second hole was formed at the opposite end measuring approximately 1 cm in diameter. Positive pressure was applied to the smaller hole, both in the form of running water and air to clear the egg contents. The interior surface of the egg was cleaned with a cotton tipped swab to insure that all egg material was voided (Rose et al., 1996). The smaller of the holes was sealed and internal volume was determined using a 50 ml buret to fill each eggshell with water.

Eggs were obtained from a captive population of *Gopherus berlandieri* (TPWD# STR-0392-504), located in San Marcos, Hays County, Texas. These were measured, weighed and processed in the same manner as those of *S. odoratus* to determine dimensions and volume of each egg.

A previously obtained data set for dimensions of *Kinosternon flavescens* eggs (Rose, unpublished data), separated by clutch and individual egg were used for comparison to the *S.odoratus* data.

Dimensions of each egg were used in each method of volume determination – ellipsoid, cylinder and bicone (Table 1) – to determine which method was the most accurate volume estimator (Iverson and Ewert, 1991). Accuracy was determined by regression analysis using SPSS Student Version 8.0. Internal volume was used for comparative purposes as it represented the amount of water that could be contained by the eggshell.

Egg dimensions across clutches were compared within each species and data were analyzed by ANOVA using SPSS Student Version 8.0. Mean values for diameter and length were calculated along with mean elongation (length – diameter) and elongation index (length / diameter) . The elongation index was calculated for eggs of each species by dividing mean length of eggs by the mean diameter. For *S. odoratus*, a mean value for diametric, or spherical increase to obtain the same volume as elongation was determined. Length, diameter, and ellipsoid volume data from *K. flavescens* and *S. odoratus* were analyzed using a t-test. Egg shape differences and effects on volume were observed between *G. berlandieri* and *S. odoratus*.

Volume measurements for 6 female *S. odoratus* of reproductive size were included (Rose, unpublished data). Mean clutch volume was divided by mean

Table 1. Mathematical equations used for volume estimation (Preston, 1974; Iverson and Ewert, 1991)

	Equation(s)	Variables
Cylinder	Sphere- $V = 4/3\ \Pi\ b^3$ Cylinder- $V = (\Pi/4)ab^2$	b = radius of the short axis a = radius of the long side axis
Ellipsoid	$V = 4/3\ \Pi\ ab^2$	b = radius of the short axis a = radius of the long side axis
Bicone	$V = 4/3\ \Pi\ ab^2 \left(\frac{3c^2 + 14c + 35}{35} \right)$	b = radius of the short axis a = radius of the long side axis *c = measure of bluntness
*c parameter	$C = ([(6.3\text{x}10^3 V / \Pi\ LW^2) - 56]^{1/2} - 7)/3$	V = volume L = long side (length) W = diameter (short side)

female volume to determine volume investment per female and for comparison to *G. berlandieri* values.

Volume was determined for two female *G. berlandieri* from the San Marcos population. Individuals were placed in a large glass cylinder of water and displacement was measured in mm. This measurement was used as cylinder height to determine tortoise volume. Mean clutch volume for this species then was divided by mean female volume to determine volume investment per female.

RESULTS

Mean number of eggs per clutch for *Sternotherus odoratus* (n = 11) was 2.7 ± 0.47 eggs. Mean egg diameter (n = 32) was 16.3 ± 0.76 mm. Mean egg length was 28.1 ± 1.73 mm. Mean internal volume was 3.9 ± 0.57 ml. Mean elongation was 11.8 ± 1.34 mm and elongation index was 1.7. The c-parameter used in the bicone formula was 0.3 ± 0.00.

Mean eggs per clutch (n = 7) for *Gopherus berlandieri* was 3.0 ± 0.94. Mean egg diameter (n = 20) was 35.6 ± 1.21 mm. Mean egg length was 41.4 ± 3.83 mm. Mean internal volume was 26.2 ± 3.79 ml. Mean elongation was 5.9 ± 4.11 mm and elongation index was 1.2. The c-parameter used in the bicone formula was 0.1 ± 0.03.

Mean number of eggs in each clutch for *Kinosternon flavescens* was (n = 9) 3.8 ± 1.3 eggs. Mean egg diameter was (n =34) 16.7 ± 0.91 mm. Mean egg length was 28.1 ± 1.76 mm. Mean ellipsoid volume was 3.9 ± 0.55 ml. Elongation index for this species was 1.7 and mean elongation was 11.8 ± 1.57 mm.

Analysis of variance for egg dimensions across clutches of *S. odoratus* eggs indicated no statistically significant difference in diameter ($p > 0.10$).

Significant differences were found in comparative length ($p < 0.05$) and volume ($p < 0.05$). Likewise in *G.* berlandieri, there was no significant difference in diameter ($p > 0.10$) nor in volume ($p > 0.10$), but there was significant difference in length ($p < 0.05$). Significant differences were found in both egg diameter ($p < 0.05$) and in length ($p < 0.05$) in *K. flavescens.*

Regression analysis of egg volume estimates for *S. odoratus* (Table 2) indicated the ellipsoid formula ($r^2 = 0.968$) and the bicone formula ($r^2 = 0.968$) were most closely correlated to internal volume measurements. The lowest correlation was seen in the use of displacement method for egg volume estimation ($r^2 = 0.863$) (Figure 1).

Regression analysis of egg volume estimates for *G. berlandieri* (Table 2) indicated the bicone formula ($r^2 = 0.924$) is most closely correlated to internal volume (Figure 2).

Eggs of *Sternotherus odoratus* and *K. flavescens* were determined to be significantly different in diameter (t-test $p < 0.05$), but differences in egg length between the two species were not significant ($p > 0.05$). When the ellipsoid method of volume estimation was used to indicate volume, there was no significant difference in egg volume between *S. odoratus* and *K. flavescens* ($p > 0.05$).

Mean volume of *S. odoratus* females was 76.8 ± 48.65 ml. Mean clutch volume was 9.8 ± 3.78 ml. Mean clutch volume was 12.8% of female turtle volume. Mean volume of *G. berlandieri* females was 1011.4 ml ± 122.61 ml.

Table 2. *Sternotherus odoratus*: Correlation coefficient (r^2) is equal in ellipsoid and bicone methods. Error is smaller and β_1 value lower for the ellipsoid calculation.

	r^2	MSE	($p\ \beta_0$)	β_0	β_1
Displace	0.863	.06225	0.656	-.015	1.083
Cylinder	0.919	.03724	0.207	0.321	1.124
Bicone	0.968	.01314	0.184	0.201	1.087
Ellipsoid	0.968	.01014	0.166	0.184	0.957

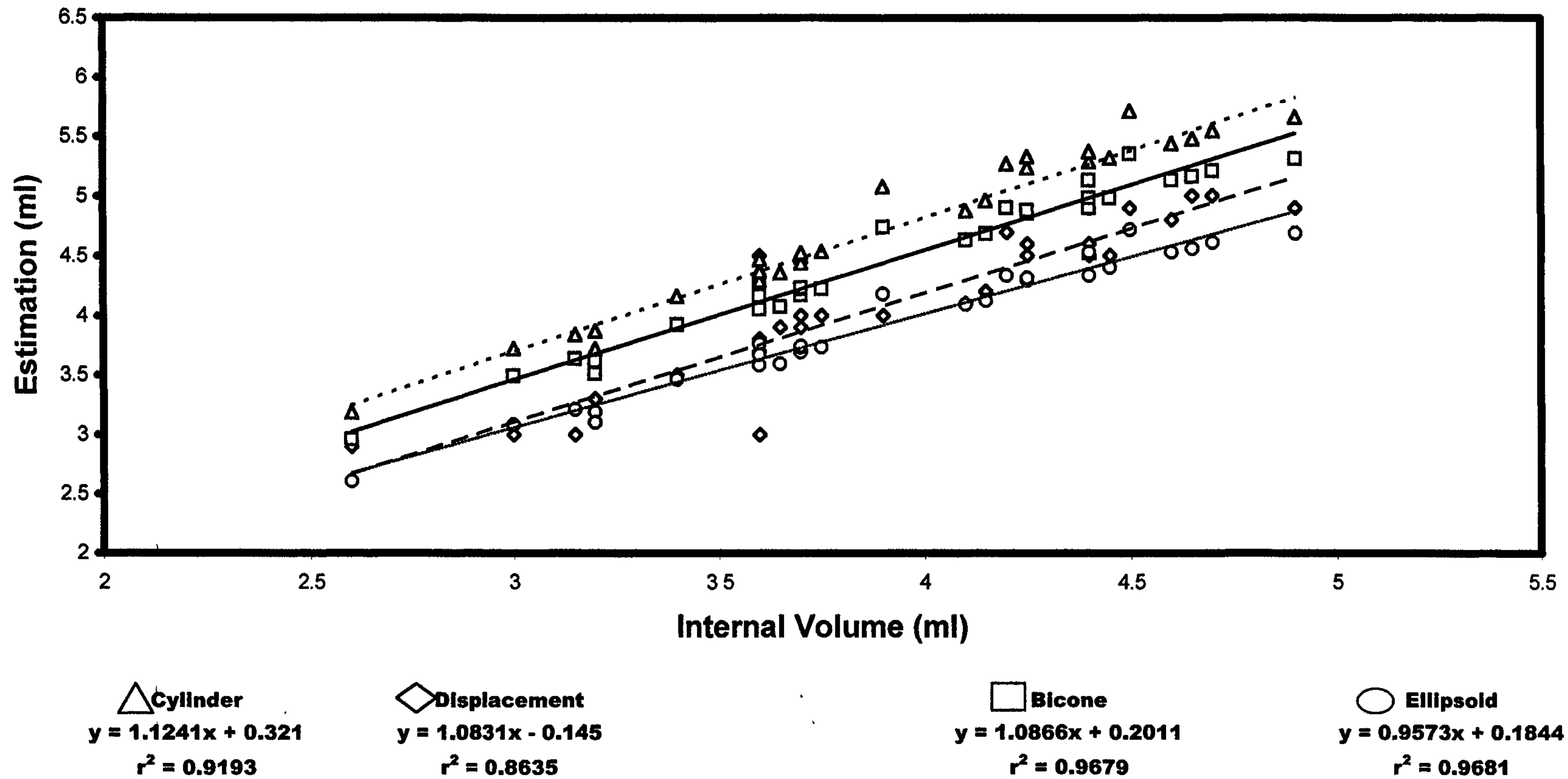

Figure 1 – Comparison of estimation methods to internal volume. Correlation coefficient (r^2) in ellipsoid formula and in bicone formula are highest. Displacement has the lowest coefficient, but still can be utilized.

Table 3. *Gopherus berlandieri:* Correlation coefficient (r^2) is higher for bicone method, error also is smaller. Value for β_1 , however, is lower for ellipsoid method.

	r^2	MSE	$(p.\beta_0)$	β_0	β_1
Displace	0.585	17.52	0.094	-17.38	1.791
Cylinder	0.868	2.422	0.249	3.986	1.006
Bicone	0.924	1.173	0.093	4.202	0.957
Ellipsoid	0.897	1.358	0.050	5.423	0.867

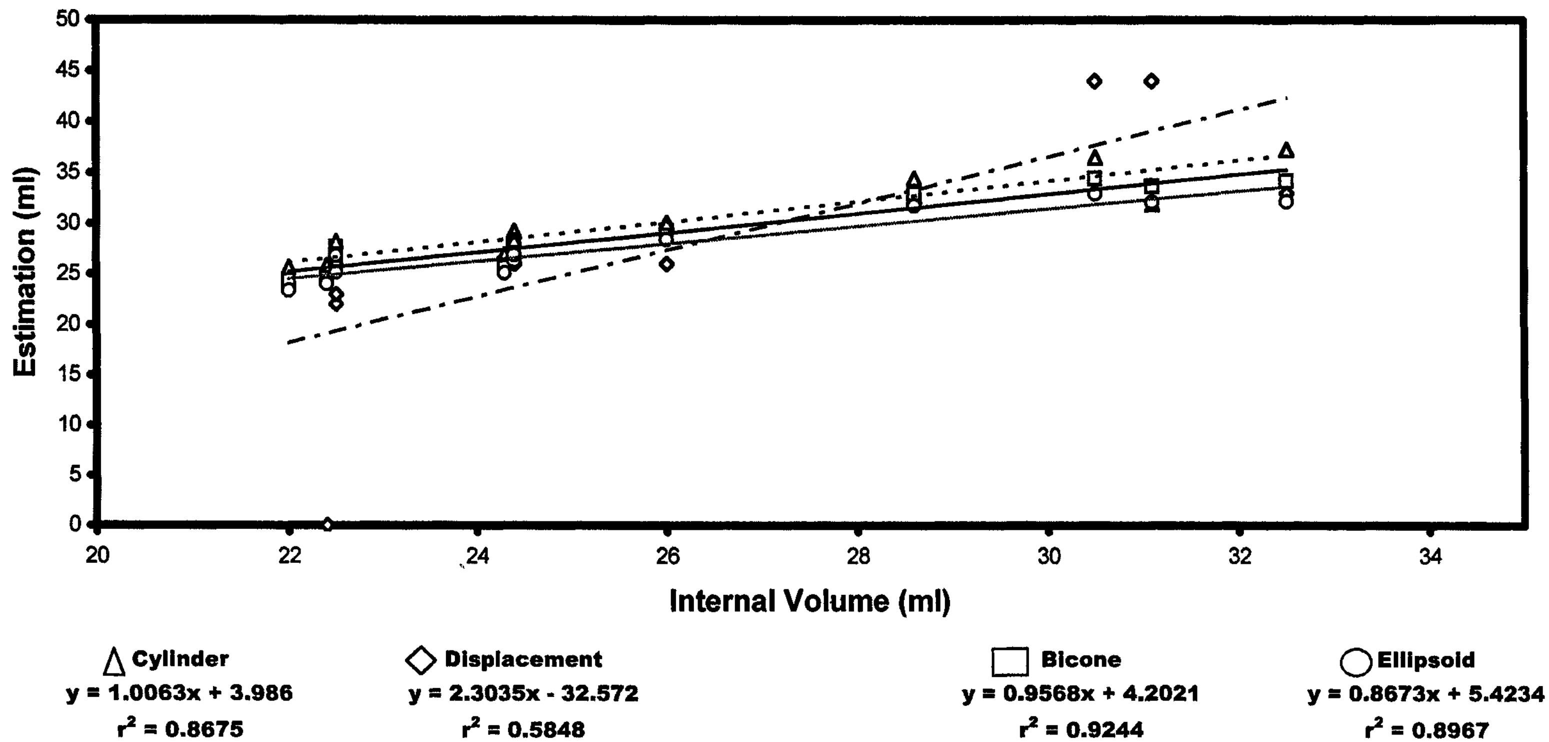

Figure 2. Comparison of each estimation method to internal volume in *Gopherus berlandieri*. Correlation coefficient (r^2) is highest for the bicone method and lowest for the cylinder method.

Mean clutch volume was 77.8 $\pm$ 23.46. Mean clutch volume was 7.6% of mean female turtle volume.

DISCUSSION

In order to adequately address reproductive parameters of oviparous species, it is imperative to know the number and volume of products (eggs) and the period of time over which production occurred. The volume of the products is a consequence of their shape and dimensions. However, reproductive output also includes total number of eggs laid in a clutch. Clutch sizes in *Sternotherus odoratus* and *Gopherus berlandieri* are well known and, although females differ in body size, both species produce one to four brittle-shelled eggs. These eggs are of radically different shape and size. Eggs of *S. odoratus* have an elongation index of 1.7, and those of *G. berlandieri* 1.2. These two species, thus, provided the opportunity to compare the accuracy of a variety of volume estimation methods, both mechanical and mathematical. As a result, further sacrifice of embryos will be unnecessary for determination of egg volume.

Egg volume represents the total space allocated per offspring for energy storage during embryo development. Ewert (1979) determined that, when broken down into major constituents, 84.8% of fresh egg weight consisted of internal components (44.7% albumin and 40.1% yolk). Volume determination allows fresh egg weight estimation and amount of yolk at the outset can be related to hatchling weight and conversion. Fresh egg weight estimation is difficult to obtain directly due to loss of water immediately upon laying.

Diameter of *S. odoratus* eggs were consistent across clutches. Length measurements, however, were significantly different indicating a larger reproductive product facilitated by elongation. This was supported further by variable volume between clutches in this within this species. For example, mean elongation was 11.8 mm while an volume could have been accomplished by increasing the short-side diameter only 3.1 mm. Clutch size in *S. odoratus* was 2 or 3 eggs per clutch.

The diameter of eggs from *G. berlandieri* also were dimensionally consistent across clutches in diameter, but significant differences were found in length measurements. There were no significant differences in volume between clutches, indicating consistent volume regardless of the number of eggs laid. This species has the ability to produce variable numbers of offspring with a consistent volume per clutch.

Egg volume could be adequately determined in *S. odoratus* using the ellipsoid mathematical method of estimation. With egg shape consistent, ellipsoid formula is probably adequate to determine egg volume for most species of aquatic chelonian (Rose et al., 1996). This method requires only length and diameter measurements and provides for very little disturbance to eggs. It is possible, although less accurate, to estimate volume using water displacement, but this method does require hatchling disturbance and decreases survival of embryos. When using the correlation coefficient (r^2) it appears that the bicone method is as accurate as the ellipsoid method, but when error is considered (MSE) the ellipsoid method is more precise. The ellipsoid method is best for determining volume in species such as *Chelydra serpentina* (common snapping turtle) and *Chrysemys picta* and has been found to be equivalent to the bicone method in *Sternotherus carinatus* (razorback turtle), *Kinosternon flavescens* and *Graptemys geographica* (common map turtle) (Iverson and Ewert, 1991).

In *G. berlandieri* eggs, internal volume was most accurately estimated by the bicone mathematical method, the correlation coefficient was higher in this method and it is necessary to use this more complex equation. According to Preston (1974) volume is determined by contour and cannot be estimated from only two measurements. In this terrestrial species, multiple parameters must be included to account for the varied nature of egg shape.

When comparing egg clutch dimensions in *S. odoratus* and *K. flavescens*, only diameter measurement was significantly different. *Kinosternon flavescens* is a larger turtle and it follows that eggs are less morphologically constrained and therefore larger in diameter. Comparisons in individual eggs of each species indicate that there is no significant difference in length or in ellipsoid volume values. Eggs of this species are of comparable volume to those of *S. odoratus*, but egg clutches in *K. flavescens* average approximately one more egg resulting in greater volume per clutch.

The percentage of female volume represented by clutch volume was two times higher in *S. odoratus* than it was for *G. berlandieri*. This could be indicative of a higher reproductive investment made by the smaller turtle. Further research and larger sample size in this area is necessary to make conclusions.

It is possible that the variation in volume in *S. odoratus* clutches is due to variation in maternal volume. In order to determine this, it will be necessary to identify individual clutches with the females that laid them and determine volume of the female turtle by water displacement. This also could be done with *G. berlandieri.* Ratios of female volume to clutch volume could be determined in order to compare energy expenditure between species.

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